

TEMPERATURE-RELATED BEHAVIOR OF SOME MIGRANT BIRDS IN THE DESERT

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ABSTRACT.— Behavior of migrant birds in relation to temperature was studied and compared to that of resident species in the northern Mojave Desert. Migrants reduced foraging intensity above 30 C, but resident species showed no striking decrease in intensity of foraging at temperatures up to 35 C. Migrant species shifted activities to shaded microhabitats at temperatures between 20 and 30 C; the resident Verdin showed a similar shift at 35 C. Most migrants decreased the amount of time spent foraging at temperatures above 30; Verdins showed a similar but stronger response to temperatures about 30 C. Significant reductions in the use of hovering and hawking maneuvers were found among migrants at temperatures above 30 C. Migrants showed similar types of behavioral adjustments to temperatures as did resident desert species, but they responded earlier in the daily temperature cycle. Desert birds appear to correlate their daily activity strongly with temperature, but nondesert species may respond either to temperature or time of day.

Several studies have shown that resident desert birds react behaviorally to high ambient temperatures by shifting activity to cooler, shaded microhabitats and reducing the intensity and amount of activity (Smith 1967, Calder 1968, Ricklefs and Hainsworth 1968, Ohmart 1969, Austin 1976, 1978). Similar reductions in activity at high temperatures were found for certain nondesert species (Ricklefs 1971, Schartz and Zimmerman 1971, Verbeek 1972). It is unknown whether the midday depression in activity from a wide variety of temperature regimens is correlated with temperature or with time of day. Among certain desert species, this depression in activity is clearly a function of temperature (Ricklefs and Hainsworth 1968, Austin 1976).

Migrant birds in the desert, especially in fall, are exposed to temperatures that exceed considerably those encountered either on the breeding or wintering grounds. The potential lethality of desert heat and aridity was documented by Miller and Stebbins (1964). To migrate successfully through the desert may require physiological and behavioral adjustments by the species involved. Behavioral differences between migrant wood warblers (Parulidae) seen at cooler, higher elevations and those seen on the desert floor were noted previously by Austin (1970). This study

was designed to detect and quantify behavioral changes over a range of temperatures by small passerine migrants during fall in the northern Mojave Desert.

METHODS

Areas frequented by migrants were visited periodically throughout the peak migration period from 20 August to 25 September 1975. These included sites near Las Vegas, Tule Springs Park, Corn Creek Field Station of the Desert National Wildlife Range, and Moapa Valley, all in Clark Co., Nevada, and at Beaver Dam Wash, Mohave Co., Arizona. Most data on migrants were obtained at Tule Springs and Corn Creek, where numerous deciduous trees have been planted. Data on resident species and on a few migrants were obtained in natural desert riparian vegetation dominated by mesquite (*Prosopis juliflora*) near Las Vegas and at Corn Creek.

When a bird was encountered, the following data were recorded: species of bird; amount of time spent in each of several activities (sitting, preening, flying, foraging), timed with a stopwatch; amount of time spent in either shade or sun; number of perch changes per stopwatch-timed interval; number of each foraging maneuver (glean, hover, hawk as described by Root 1967); time of day

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and air shade temperature (T_a 's noted on the half h). Several problems were encountered by the observer while following the individual bird under observation; the most notable of these was keeping track of the individual, which was often among several conspecifics. This situation, and the fact that migrants rarely remained in sight for long periods, resulted in most observations being of 3–5 minutes or less duration. Mean values and percentages were calculated using all periods of observation regardless of duration. Only observations greater than 1 minute in length were subjected to further statistical analysis.

Foraging maneuver data were treated with chi-square goodness of fit on the numerical data using Yates's correction where applicable. Feeding activity as perch changes per min and microhabitat usage expressed as proportion of time (transformed to arcsine; Zar 1974) spent in shade were analyzed using polynomial regression analysis. Diversity of foraging maneuvers and partitioning of time for T_a 's above and below 30 C were calculated using the information-theoretical measure to the base e (H'). Differences between H' at the two temperature ranges were tested using the methods outlined in Zar (1974). Statistical significance was set at $P \leq 0.05$ throughout.

Principal species studied were (minimum number of individuals observed are in parentheses): Warbling Vireo (*Vireo gilvus*) (20) and the warblers: Orange-crowned (*Vermivora celata*) (32), Nashville (*V. ruficapilla*)

(25), Yellow (*Dendroica petechia*) (68), MacGillivray's (*Oporonis tolmiei*) (30), Wilson's (*Wilsonia pusilla*) (37), and American Redstart (*Setophaga ruticilla*) (7). Additional small samples (less than 50 minutes and 10 individuals) were obtained for other migrant and some resident species that will be mentioned in the text. Data were also obtained for the resident Verdin (*Auriparus flaviceps*); these were combined with data gathered for other studies (Austin 1976, 1978). Total sample for Verdins was approximately 30 individuals. Total amount of timed data for each temperature range is given in Table 1. Data collection was facilitated by the use of tape recorders. Observations were made on clear days under low wind conditions (< 8 km/h).

RESULTS

FORAGING RATE.— Rate of foraging by migrant species was comparatively rapid at T_a 's below 30 C and sharply less rapid above 30 C (Table 2). On the average, foraging by migrant warblers was reduced by 10 perch changes per minute (37 percent) above 30 C. Greatest reductions were by Orange-crowned and Nashville warblers (43 and 47 percent). Analysis of these data by 2 C intervals indicated that 30 C was a well-defined point where foraging rate changed abruptly. Rate of foraging by Yellow Warblers, for example, average 22.1 and 15.2 perch changes per minute at 28–30 C and 30–32 C, respectively.

TABLE 1. Amount of observation time (seconds) obtained for foraging behavior.

	T_a (degrees C)				
	15–20	20–25	25–30	30–35	35–40
Verdin (V) ^a	10576	49475	45813	41179	59800 ^b
Bewick's Wren (BW)	—	403	594	1235	—
Black-t. Gnatcatcher (BTG)	—	677	460	—	201
Warbling Vireo (WV)	1039	1732	1324	1283	—
Orange-cr. Warbler (OCW)	1883	1621	3583	2371	—
Nashville Warbler (NW)	1238	1409	1050	3357	1443
Virginia's Warbler (VW)	372	772	85	426	180
Lucy's Warbler (LW)	50	789	67	1023	—
Yellow Warbler (YW)	3179	5783	8307	16475	1327
Black-th. Gray Warbler (BTGW)	132	538	48	793	—
Townsend's Warbler (TW)	1966	—	344	698	—
MacGillivray's Warbler (MW)	2323	2928	1006	3181	681
Wilson's Warbler (WW)	2071	1341	4658	5259	370
American Redstart (AR)	657	533	801	593	—

^aSpecies code in parentheses.

^b T_a = 35–50 degrees C.

Apparently this response was more a function of T_a than time of day as indicated in Table 3. Rate of foraging during midday was greater on cool days than on hot days. Early morning foraging was at a somewhat reduced rate compared to later in the day at similar T_a 's, accounting for the lower intensities at 15–20 C. Because of this, data for temperatures below 20 C were not used in regression analysis (below).

The slowly foraging Warbling Vireo showed only a slight decrease in foraging above 30 C. Its foraging rate, however, was lower than other species at all T_a 's. Among migrant species with small samples, Virginia's Warbler (*Vermivora virginiae*) exhibited a gradual decrease in foraging with increasing T_a . American Redstart decreased foraging rate dramatically (by 44 percent) at 30 C and Townsend's Warbler (*Dendroica townsendi*) decreased foraging at about 25 C. The migrant Black-throated Gray Warbler (*D. nigrescens*) and the resident Bewick's Wren (*Thryomanes bewickii*), Black-tailed Gnatcatcher (*Poliptila melanura*), and Lucy's Warbler (*V. luciae*) apparently do not reduce foraging through at least 35 C. The Verdin exhibited a gradual decrease in rate of foraging with increasing T_a (Table 2; Austin 1976: Fig. 6); the most dramatic decrease (45 percent) was at 35 C.

Although the individual observations show considerable variability at all T_a 's, foraging rates of the various species exhibit significant negative linear or quadratic relationships with T_a (Table 4). Although the variability involved is real on a short-term basis, we believe that the averages for each temperature range (Table 2) reflect a true and biologically

important adjustment by these birds as T_a increases. Samples obtained over longer periods of time on an individual tend to show less variability, as indicated previously for the Verdin (Austin 1976).

MICROHABITAT USAGE.—Migrant species varied in the relative amount of time spent in shaded or exposed microhabitats (Fig. 1). MacGillivray's and Wilson's warblers foraged largely in the shade at all T_a 's but especially at higher T_a 's. In other transients, the proportion of time spent foraging in the shade was not as great at lower T_a 's and increased rapidly with T_a . Warbling Vireos and Yellow Warblers made the most abrupt shift to shaded microhabitats at 30 C; Orange-crowned and Nashville warblers did so at 20 C. On the average, more than 95 percent of all foraging was in shade at T_a 's above 30 C (Fig. 1).

The resident Verdin, in contrast, did not shift its foraging to predominately shaded microhabitats until T_a exceeded 35 C (Fig. 1; Austin 1976: Fig. 5). Above 35 C, about 15 percent of its foraging was still in vegetation exposed to the sun. Data for the Black-tailed Gnatcatcher indicated a similar pattern. Bewick's Wren and Lucy's Warbler appeared to forage predominately in the shade at all T_a 's.

As with foraging rate, individual variability in microhabitat use (as proportion of time spent in shade) was great. Regression analysis of time spent in shade in relation to T_a indicated significant positive correlations for the six migrant species (Table 4). The variability and consequently low correlations for MacGillivray's and Wilson's warblers were likely due to the large number of relatively

TABLE 2. Mean number of perch changes per minute by birds in relation to ambient temperature.^a

Species	Ambient temperature (degrees C)				
	15-20	20-25	25-30	30-35	35-40
Verdin	22.0	18.2	19.4	16.6	9.1
Warbling Vireo	15.4	16.4	14.8	11.2	—
Orange-crowned Warbler	21.6	26.2	23.0	13.1	—
Nashville Warbler	18.6	21.5	26.1	13.9	10.8
Yellow Warbler	22.4	22.4	23.2	13.5	13.4
MacGillivray's Warbler	20.6	26.7	21.2	15.1	—
Wilson's Warbler	32.7	37.0	34.6	26.6	19.8
American Redstart	31.6	41.1	39.5	23.3	—

^aObservations summed for each temperature range regardless of duration of each observation; total observation time for each temperature range as indicated in Table 1.

short-duration (1–2 min) observations for these species. The statistically significant regressions, however, indicated that all six species increased the use of shade as T_a increased.

TIME BUDGET.—The partitioning of time by migrants varied with T_a . At lower T_a 's, nearly all time was spent foraging and less than 5 percent spent sitting (Fig. 2). Above 30 C, the amount of time sitting increased to about 20 percent in most species. MacGillivray's Warbler did not increase time spent in inactivity above 20 percent until T_a reached 35 C. Wilson's Warbler did not sit more than 6 percent of the time at any T_a .

The Verdin increased sitting time gradually through 35 C. Above 35 C, the amount of time sitting increased sharply to 66 percent (Fig. 2; Austin 1978). The other three resident species did not increase time spent sitting above 30 C; too few data were obtained for T_a 's above 35 C to draw conclusions.

FORAGING MANEUVERS.—At T_a 's greater than 30 C, all migrant species decreased the use of hawking and hovering foraging maneuvers (Fig. 3). This change in foraging strategy above and below 30 C was statistically significant in all species except Black-throated Gray and MacGillivray's warblers

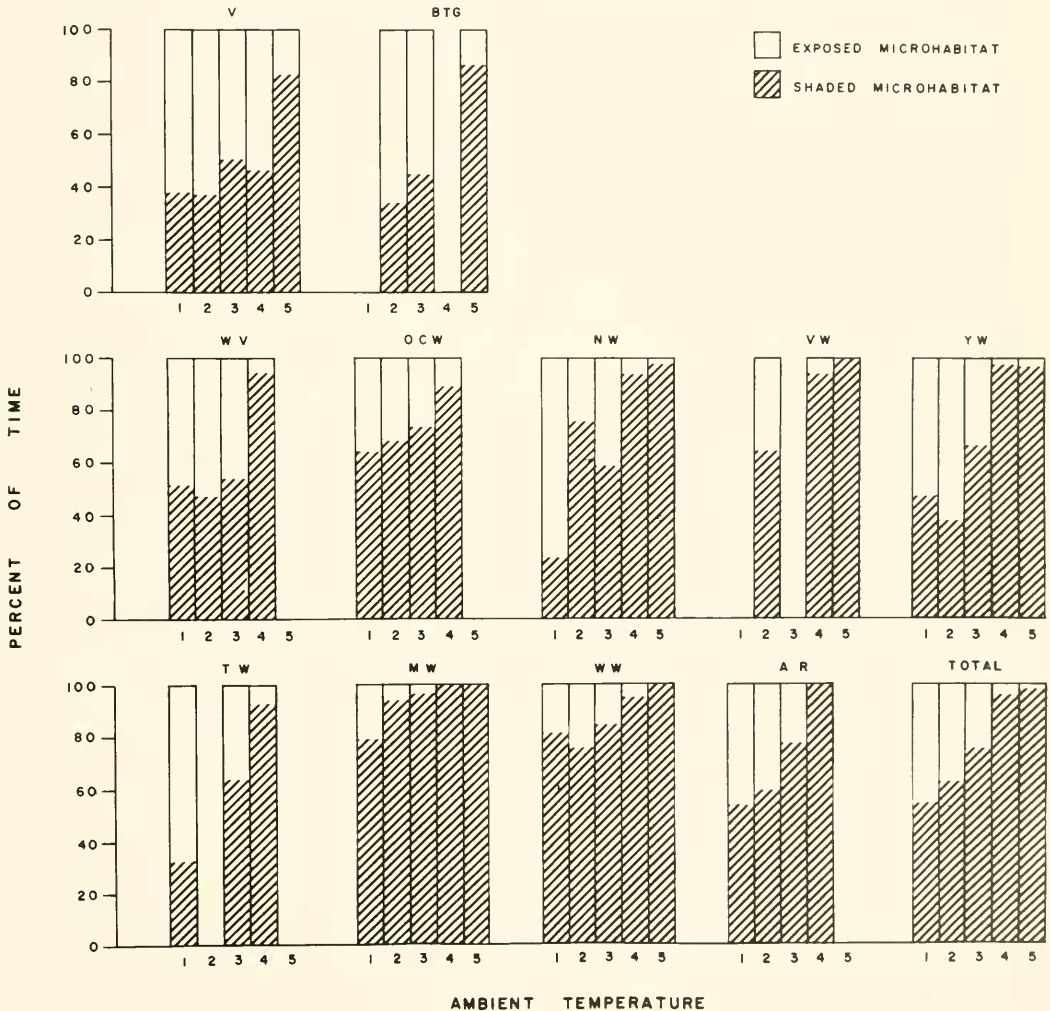


Fig. 1. Percent of time spent in shaded and exposed microhabitats as a function of ambient temperature by migrant and resident birds in southern Nevada. Temperature code is as follows: (1) 15–20 C, (2) 20–25 C, (3) 25–30 C, (4) 30–35 C, (5) 35–40 C. Species indicated by letters above bars are as coded in Table 1.

and was especially striking in Wilson's Warbler and American Redstart. Overall, both hawking and hovering were reduced proportionately, but Wilson's Warbler reduced hovering to a greater extent than hawking. When all three types of maneuvers were considered independently, Warbling Vireo, Yellow and Wilson's warblers, and American Redstart exhibited significant changes in overall foraging behavior. Larger samples for other species may show similar differences.

Samples for any one of the resident species were too small for analysis. The pooled data for the four species, however, showed no change in foraging strategy over the range of T_a 's sampled.

DISCUSSION

Migrant species of birds showed behavioral changes at high temperatures that were similar in kind to those of resident species. Both reduced the amount and rate of foraging and shifted their activities to cooler microhabitats as ambient temperatures increased. Such changes in behavior reduce metabolic and environmental heat gain. In migrants the shift to cooler microhabitats tended to precede reduction in foraging rate, as was previously found for residents (Ricklefs and Hainsworth 1968, Austin 1976). This allows reduced heat stress but continued high rates of foraging. Changes in behavior were apparently more closely related to temperature than to time of day.

Although migrants were similar to resident desert species in the types of behavioral changes with increasing temperature, there were obvious differences in the temperature at which these occurred and the magnitude of change. Among resident species, foraging was reduced only at T_a 's exceeding 35 C. Migrants generally decreased foraging rates at

about 30 C. Similarly, there was an abrupt change in the partitioning of time by migrants at 30 C and by residents at 35 C. A shift to shaded microhabitats occurred in migrants at T_a 's ranging between 20 and 30 C. Residents did not greatly increase the use of shade until T_a 's exceeded 35 C.

At T_a 's exceeding 35 C, the resident Verdin drastically reduced the amount of time spent foraging to less than 35 percent. No migrant species decreased foraging to less than 70 percent. This suggests that migrants may have to continue foraging at high T_a 's to replenish energy stores and to maintain water balance, or that their adjustments to T_a are less refined than those of residents. The migrants' unfamiliarity with local conditions may also, in part, account for the increased foraging time. In any case, it seems likely that migrants need access to free water or an abundant food source during passage through the desert, which accounts for their relative rareness in the low desert away from riparian habitats.

Table 5 shows that diversity of foraging maneuvers decreased in all species at T_a 's above 30 C; these differences were significant for all species except MacGillivray's Warbler. This decrease in diversity reflects the reduction of maneuvers involving flight (Fig. 3). Diversity in the partitioning of time increased significantly at T_a 's above 30 C (Table 5). This reflected the increased amount of time spent resting at higher T_a 's, whereas nearly all time was occupied by foraging at the lower T_a 's (Fig. 2). Extreme weather conditions were shown by Grubb (1975) to affect foraging diversity of birds in eastern deciduous forest.

Diurnal rhythms in foraging behavior have long been recognized in birds (e.g., Palmgren 1949). It is generally recognized that there is a peak of activity in the morning that

TABLE 3. Foraging rate (number of perch changes per minute) as a function of T_a and time of day.

Species	Time	0600-1000		1000-1400		1400-1800	
	T_a	< 30 C	< 30 C	> 30 C	> 30 C	> 30 C	> 30 C
Orange-crowned Warbler		22.9	24.2	14.3	12.5		
Nashville Warbler		19.4	23.1	14.0	12.8		
Yellow Warbler		21.5	27.3	16.9	13.8		
MacGillivray's Warbler		22.3	26.2	15.1	—		
Wilson's Warbler		34.2	35.1	26.0	17.4		

decreases toward midday and often increases again to another peak at the end of the day. In some species, this appears as a circadian rhythm, occurring at the same time of day under constant light conditions, as in the Arctic (Armstrong 1954) and under constant temperature conditions in the laboratory (Eyster 1954, Coutlee 1968, Smith et al. 1969). High temperatures modified this behavior in at least the White-crowned Sparrow (*Zonotrichia leucophrys*); activity at 33 C was 50 percent of that at 23 C. Daily activities of the House Sparrow (*Passer domesticus*) and Dark-eyed Junco (*Junco hyemalis*), however, were affected little at temperatures as high as 32 C and 35 C, respectively (Eyster 1954).

Field studies have demonstrated that a number of nondesert bird species reduce activity at high temperature. In the post-breeding Yellow-billed Magpie (*Pica nuttalli*), the amount of time spent foraging was negatively correlated with temperatures above approximately 25 C (Verbeek 1972). The male Dickcissel (*Spiza americana*) decreased various behaviors associated with reproduction and increased the amount of time spent resting as temperatures increased above 35 C (Schartz and Zimmerman 1971). Although total time spent foraging seemed unaffected, foraging intensity was reduced. The midday decrease in foraging time by the tropical Mangrove Swallow (*Iridoprocne albilinea*) was also suggested to be due to high radiational heat loading coupled with high

humidity (Ricklefs 1971). Tropical flycatchers and Temperate zone swallows showed little or no reduction in midday activities (Ricklefs 1971).

Several desert species showed a close correlation between a reduced rate of activity or increased use of shaded microhabitats and increasing temperature (Dawson 1954, Smith 1967, Calder 1968, Ricklefs and Hainsworth 1968, Ohmart 1969, 1973, Austin 1976, 1978). Most species are highly active at midday in the cooler months of the year or on cool, cloudy days during midsummer. Behavioral changes observed in these studies may be actual adjustments in direct response to T_a , an indirect reflection of changes in distribution and activity of prey items or a combination of them. The available data suggest the latter. The Roadrunner (*Geococcyx californianus*) maintained approximately constant rates of activity throughout the day in the laboratory at moderate temperatures (Kavanau and Ramos 1970). In the field, well-defined periods of inactivity in shaded areas were apparent during hot middays (Calder 1968, Ohmart 1973). Time of foraging was correlated with peak activity of their principal prey (Ohmart 1973). Captive Cactus Wrens (*Campylorhynchus brunneicapillus*) decreased activity and increased amount of time spent in shade with increasing T_a with food equally available under all conditions (Ricklefs and Hainsworth 1968). These changes in behavior were similar to those

TABLE 4. Regression analyses of the relationships between ambient temperature ($X = T_{a,b}$) and foraging intensity ($Y =$ perch changes per min)^a and proportion of time spent in shaded microhabitat ($Y =$ arcsine of the proportion) by some migrant birds in the Mojave Desert.

Species	Dependent variable (Y)	Number of observations ^c	Correlation coefficient	Regression formula
Warbling Vireo	perch changes/min	25	0.477	$Y = 29.20 - 0.53X$
	% of time in shade ^b	21	0.558	$Y = -27.70 + 3.19X$
Orange-crowned Warbler	perch changes/min	33	0.695	$Y = 57.98 - 1.27X$
	% of time in shade ^b	35	0.652	$Y = -22.81 + 2.98X$
Nashville Warbler	perch changes/min	42	0.646	$Y = -155.97 + 13.01X - 0.24X^2$
	% of time in shade ^b	25	0.696	$Y = -6.45 + 2.71X$
Yellow Warbler	perch changes/min	100	0.500	$Y = 43.41 - 0.82X$
	% of time in shade ^b	81	0.661	$Y = 188.01 - 13.20X + 0.30X^2$
MacGillivray's Warbler	perch changes/min	36	0.514	$Y = 45.87 - 0.89X$
	% of time in shade ^b	33	0.351	$Y = 60.29 + 0.75X$
Wilson's Warbler	perch changes/min	71	0.467	$Y = 66.47 - 1.20X$
	% of time in shade ^b	41	0.442	$Y = 25.68 + 1.65X$

^aOnly data for ambient temperatures greater than 20 C were used, because foraging intensity was reduced in early morning at lower temperatures.

^bRelationship expressed as arcsine $Y =$ arcsine $a + bX$.

^cOnly observations > 1 min in length were used in regression analysis (see text).

observed in the field. Data on insects indicate that they reduce their activity and move into shaded microhabitats in response to increasing temperature (e.g., Clench 1966, Austin 1977).

Aside from differences in prey distribution and activity and temperature, other factors may account for some of the variability observed in behavioral modifications. The amount of time spent resting by the Dickcissel increased more rapidly at high T_a 's when relative humidities were greater (Schartz and Zimmerman 1971). In the Las Vegas area during August and September, relative humidities average below 20 percent during daylight hours (Brown 1960) and are unlikely

to be a major factor affecting behavior. Wind also affects bird behavior (Grubb 1975). In this study, however, observations were not made when the wind exceeded 8 km/h (most were taken on completely windless days), so wind is considered a constant.

Two distinct thermoregulatory problems arise when contending with desert heat; heat loading is often severe and, although low humidities promote effective evaporative cooling, water is largely unavailable. Species occurring in the desert are thus faced with opposing problems of water conservation and maintenance of heat balance. Such behavioral adjustments as shifting to shaded microhabitats and eventually reducing the intensity

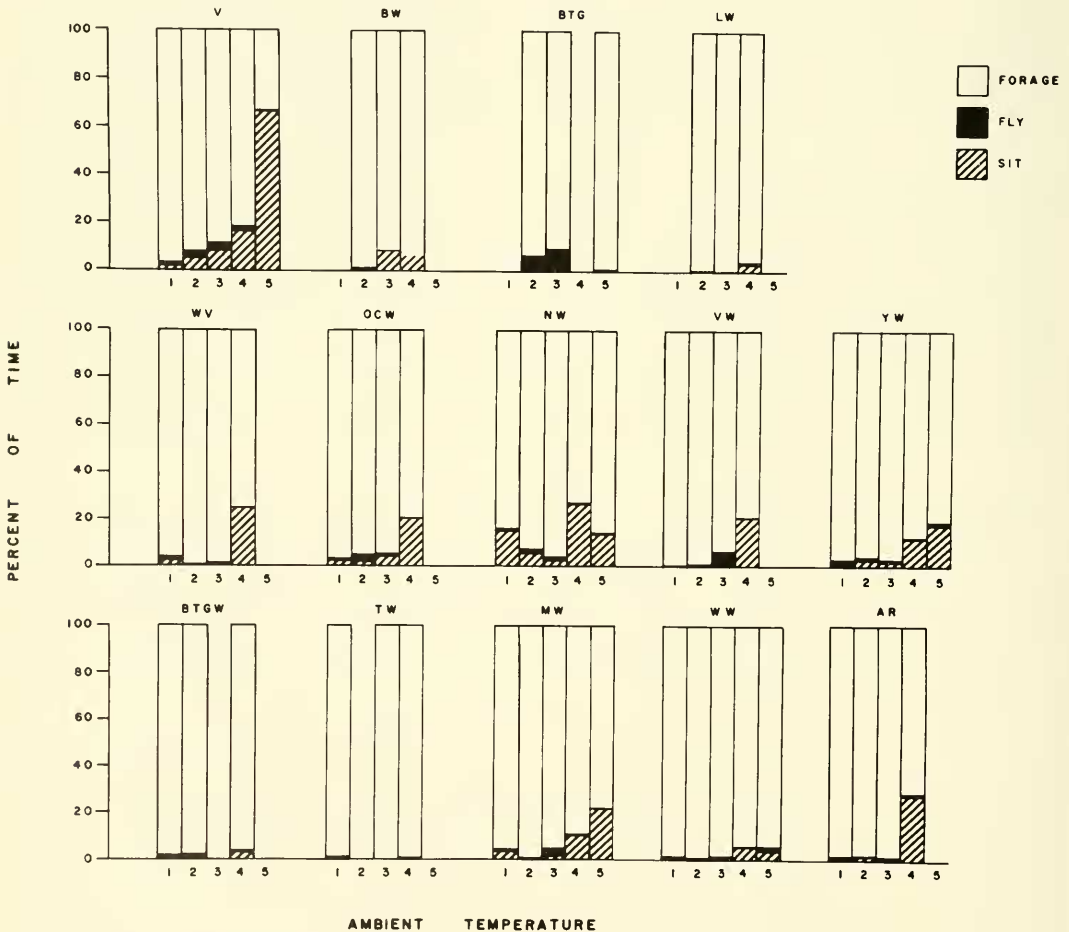


Fig. 2. Time budget of migrant and resident birds as a function of ambient temperature in southern Nevada. Temperature and species code as in Fig 1.

and amount of activity to a minimum may be a necessary and important means of contending with high temperatures. In non-arid localities behavioral means of reducing heat load may also be of some importance but for a different reason. Although temperatures tend to be lower than in arid areas, relative humidities are usually higher. This increased humidity reduces the effectiveness of evaporative cooling mechanisms due to a decrease in the vapor pressure gradient. Further studies of bird behavior under varying humidity conditions are highly desirable.

ACKNOWLEDGMENTS

We thank W. G. Bradley, K. S. Moor, S. Naegle, R. D. Ohmart, R. E. Ricklefs, D. Thomas, and J. L. Zimmerman for suggestions on statistical procedures or comments and suggestions for improvements of the manuscript.

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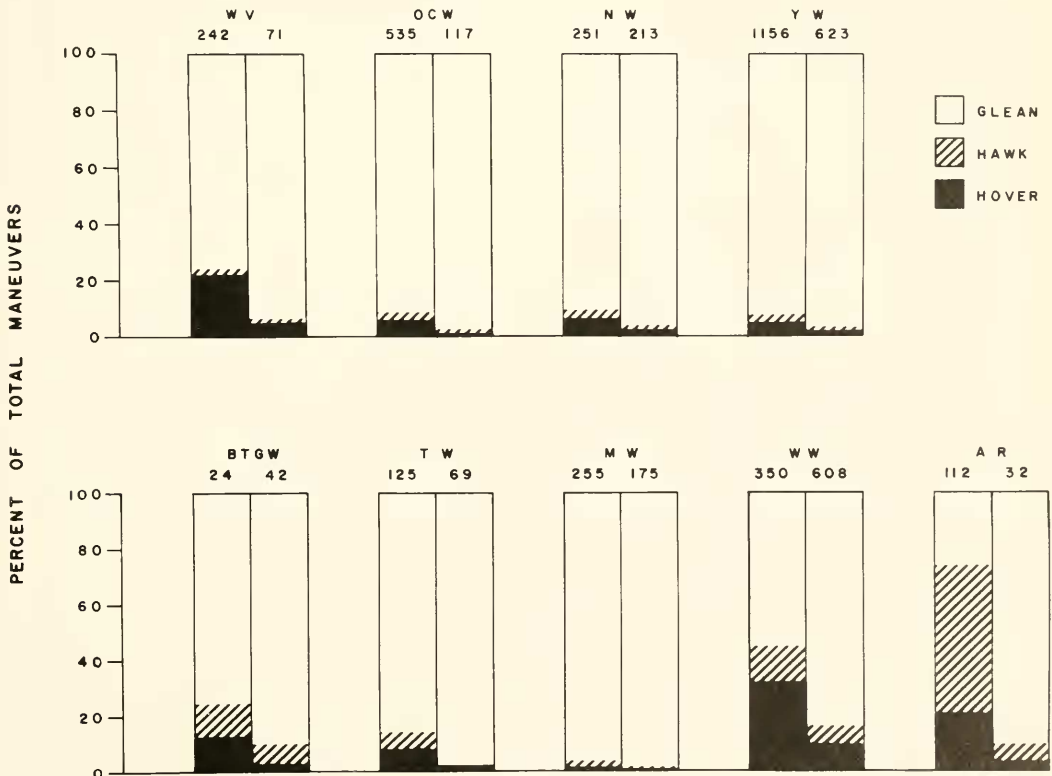


Fig. 3. Changes in the use of various foraging maneuvers as a function of ambient temperature by migrant birds in southern Nevada. Left-hand bar for each species represents temperatures less than 30 C; right-hand bar represents temperatures greater than 30 C. Species code as in Fig. 1. Number of foraging maneuvers observed indicated above each bar.

TABLE 5. Indices of foraging diversity (H') by migrant birds in relation to temperature. Maximum diversity for 3 alternatives = 1.099 (to the base e).

Species	Time budget at T_a		Foraging maneuvers at T_a	
	< 30 C	> 30 C	< 30 C	> 30 C
Warbling Vireo	0.087	0.263	0.621	0.290
Orange-crowned Warbler	0.219	0.539	0.359	0.136
Nashville Warbler	0.340	0.584	0.376	0.185
Yellow Warbler	0.200	0.418	0.329	0.157
MacGillivray's Warbler	0.150	0.419	0.177	0.098 ^a
Wilson's Warbler	0.080	0.256	0.961	0.567
American Redstart	0.112	0.661	0.949	0.371

^aDifference not significant.

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